

ENVIRONMENTAL FACTORS IN RELATION TO THE SALT CONTENT OF *SALICORNIA PACIFICA* VAR. *UTAHENSIS*¹

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ABSTRACT.— The stability of the salt content in *Salicornia pacifica* Standl. var. *utahensis* (Tidestrom) Munz in relation to environmental changes was investigated. *Salicornia pacifica* communities have a characteristic soil pH of 7.5 to 8.0 \pm 0.2 and a constant subsurface soil moisture level of 25 to 35 percent. The ion content in the tissue of *S. pacifica* remained constant despite increased moisture stress throughout the growing season. The concentrations of the salts were significantly higher in the surface soil layers than in the subsurface layers around the roots. Normal metabolic processes in the tissues of *S. pacifica* appear to occur even though some fluctuations in the ionic balance and concentration of ions in the plant occur.

Introduction

Halophytic plants are among the few species of higher plants that can withstand high saline soil conditions without detrimental effects (Waisel, 1972). The is mainly associated with an increase in the chloride content of the tissues (Adriani, 1958; Bernstein, 1961). Steiner (1935) found that chloride ions accounted for 67 to 88 percent of the increase of osmotic potential of different species of salt marsh plants, whereas other osmotically active substances had only a negligible effect. Chloride accounted for 80 percent of the total osmotic potential in *Salicornia ambigua*, 91 percent in *S. stricta*, and 93 percent in *S. mucronata* (Arnold, 1955). Harward and McNulty (1965), on the other hand, found that chloride accounted for less than 49 percent of the osmotic potential in *S. rubra*.

Osmotic values for leaf saps of a number of herbaceous halophytes including *S. herbacea*, ranged from 25 to 75 atm when grown in salt marshes (Yabe et al., 1956). Seasonal changes in osmotic potentials in tissues of *S. rubra* ranged from 40 atm to over 100 atm over a two-month period (Harward and McNulty, 1965). Higher osmotic potential values have been recorded for a number of halophytes; for example, Waisel (1972) reported that osmotic potentials of *Rhizophora* and *Avicennia* leaves reached values of 148 and 163 atm, respectively.

According to Bowen and Rovira (1966), salt ions can cause toxicity in the following ways: (1) acting as antimetabolites, (2) binding or precipitating various metabolites, (3) catalyzing rapid decomposition of essential elements, (4) combining

with cell membranes and affecting their permeability, and (5) displacing essential elements but failing to fulfill their functions. Bowen and Rovira (1966) suggested that salt injury is not due to a direct effect of the salts but to the indirect effects of one or more of the above mentioned metabolic disturbances. Waisel (1972) singled out nitrogen metabolism as an important area affected by high salts. Salt-induced growth retardation leads to an accumulation of unused substances that may be toxic (Gauch and Eaton, 1942).

The degree of salt injury or tolerance of plants may be affected by a number of environmental factors such as waterlogged soils. Some plants, however, have adapted to waterlogged conditions. *Salicornia foliosa* not only tolerates waterlogged conditions but appears to benefit from them, because of increased capacity to obtain iron under these conditions thereby avoiding chlorosis (Adams, 1963). In habitats with marked fluctuations in salt concentration, only the species with high osmotic shock resistance (*Salicornia* sp.) can survive (Levitt, 1972). Some of the facultative halophytes, such as *Salicornia rubra*, are found at the highest salinities yet are capable of growing normally in low to nonsaline environments (Ungar et al., 1969).

Since species of *Salicornia* are among the most salt tolerant forms of higher plants (Chapman, 1960), *S. pacifica* Standl. var. *utahensis* (Tidestrom) Munz., a halophyte common to inland salt playas of northern Utah, was selected for this investigation. Due to the lack of basic information about environmental fluctua-

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tions in *S. pacifica* habitats and difficulties in providing an artificial environment that parallels the natural environment, investigations were undertaken to correlate fluctuations of the natural environment with physiological and morphological characteristics in relation to salt content of *S. pacifica*.

Methods and Materials

This investigation was conducted during a typical growing season for *Salicornia pacifica* (April to August 1972). Three sites were selected to compare soil and moisture factors in relation to changes in salt content of *S. pacifica*. Sites 1 and 2 were six miles (9 km) north and Site 3 was about one-half mile (1 km) east of Goshen, Utah. Site 1 was especially selected because it was an ecotone between a stand of *S. pacifica* and a stand of *Distichlis stricta*. It was hoped that the data from this site could be used to explain some of the environmental factors responsible for separating the *Salicornia* communities from the *Distichlis* communities.

The ground at Site 1 was covered by a thin layer of dried algae of the genus, *Oscillatoria*. This covering formed a sur-

face mulch which increased the moisture of the soil surface. Site 2 was about 100 m west of Site 1 on the opposite side of a large drainage basin. Site 3 (Fig. 1) was 6 miles (9 km) from Sites 1 and 2 adjacent to a natural drainage system. Site 3 was selected because of reduced fluctuations in soil moisture throughout the growing season. Soil and plant samples were taken every two weeks at all three sites.

A standardized hygrothermograph unit was used to continuously monitor temperature and relative humidity. The housing unit for the hygrothermograph was located three inches above the ground about 100 m from Sites 1 and 2. Measurements were recorded from 1 May through 20 September 1972.

The percentage of plant cover for Sites 1, 2, and 3 was determined using eight randomly distributed rectangular $\frac{1}{4}$ m² quadrats. Dry weight production in each site was determined by clipping four randomly distributed rectangular $\frac{1}{4}$ m² quadrats.

Soil samples were taken with a soil core borer. Each core measured 1 inch (2.54 cm) in diameter and was extended to a depth of 10 inches (25.4 cm). The cores were separated to provide surface (upper



Fig. 1. Site 3, located one mile east of Goshen, Utah, showing a typical stand of *Salicornia pacifica* (Photograph courtesy of W. M. Hess.)

2 inches or 5 cm of the core) and subsurface (lower 6-10 inches or 15-25 cm of the core) soil samples. Five to eight core samples were taken at each site and pooled to obtain the soil sample. The samples were placed in plastic bags, sealed, and immediately taken to the laboratory for analysis. Samples were weighed to the nearest one-hundredth of a gram and dried in an oven at 110C for 48 hours. The samples were weighed again, and the percentage of moisture was calculated.

Measurements of the soil pH were determined from saturated soil paste samples using the Sargent-Welch pH Meter, Model PAX, with a combination electrode.

Osmotic potentials of soil samples were determined from saturated soil pastes by freezing-point depression methods according to the procedure outlined by Hansen and Weber (1974).

Soil samples (5 g) were leached of exchangeable cations and anions by flushing with four 25 ml volumes of 1N CH_3CO

C-NH_2 , pH 7.0. Each volume was allowed to drain before the next was applied. The cations (sodium, potassium, magnesium, and calcium) were detected in the filtrate according to procedures outlined by Perkin-Elmer (1971) on the Model 290B Atomic Absorption Spectrophotometer. The anion, chloride, was detected in the filtrate according to the procedure outlined by Marius/Fiske (1972) using a Marius/Fiske Chlor-o-counter.

Osmotic potential measurements for *Salicornia* were determined by freezing-point depression techniques as described by Cary and Fisher (1969, 1971) and Fisher (1972). The circuitry was modified by replacing the two 1.35 vdc Hg battery cells with an alkaline 9 vdc battery. A 10K 1-turn potentiometer was installed to compensate for voltage drop that oc-

curred with time and usage. Measurements were made at each internode for several plants. Measurements were occasionally made using a vapor pressure osmometer, Model 301 Mechrolab Inc., to verify freezing-point measurement values.

The percentage of crude protein in each plant sample was determined by the micro-Kjeldahl method (Horwitz, 1970).

Results

Climatic and Growth Factors

Continuous hygrothermograph monitoring of climatic factors indicated that temperatures fluctuated consistently throughout the growing season. The average temperatures gradually increased through May and June. A peak was reached during July, followed by a gradual decrease from August to September. The average of the daily highs during July was 34C. The hottest temperature in July was 38C on 12 July. The coolest temperature recorded in July was 6C on 25 July.

Lowest daily means (calculated on an hourly basis) for relative humidity occurred from 15 July through 20 August. A series of rain storms increased the relative humidity during late August and early September. Light rain was also common during late May and early June. No quantitative data concerning the amount of rain was taken. Relative humidity reached 100 percent every night except for about six days during the growing season.

The dry weight of the standing crop of *S. pacifica* plant tissue was the highest on Site 3 (141.2 g/m²) and the lowest on Site 2 (26.7 g/m²) as shown in Table 1. The percentage cover was also highest on Site 3 (65 percent) and lowest on Site 2 (7.5 percent). The percentage moisture of the plants in all three sites was about 80 percent.

Soil Moisture

The subsurface and surface soil moisture readings for Site 2 were highest during June, gradually decreasing throughout the growing season (Fig. 2). The subsurface soil moisture for this site was less than the surface soil moisture from 1 April through 15 July. This may have been due to the heavy mulch of algae on the surface. However, from mid-July through the rest of the season, this trend

TABLE 1. Percentage moisture, dry weight production, and percentage cover of *Salicornia pacifica* in three salt desert plays.

Site	Percentage moisture	Dry weight production g/m ²	Percentage cover
1	79.0	73.1	56.0 <i>S. pacifica</i> 2.5 <i>S. rubra</i>
2	80.6	26.7	7.5 <i>S. pacifica</i> 1.0 <i>A. occidentalis</i>
3	80.6	141.2	65.0 <i>S. pacifica</i> 2.5 <i>S. rubra</i>

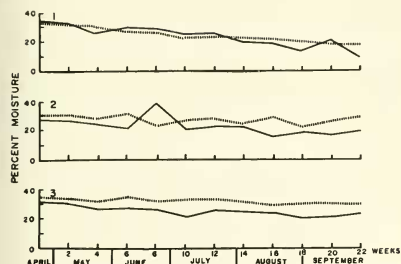


Fig. 2. Soil moisture for three salt desert playas (Sites 1, 2, and 3). Solid lines indicate the plot of percentage values for surface soil samples (upper 2"). Dashed lines indicate the plot of percentage values for subsurface soil samples (6-10").

was reversed. In Sites 2 and 3 the subsurface soil moisture was consistently higher than the surface soil moisture throughout the growing season, except for one week in June when Site 2 had an increase in the surface soil moisture due to rainfall. Surface and subsurface soil moisture percentages at Site 3 were well above moisture percentages of Sites 1 and 2. From June through July soil moisture in Site 3 was above 30 percent, whereas soil moisture of Sites 1 and 2 was well below 30 percent. This was probably due to underground seepage from the nearby drainage system adjacent to Site 3. Soil moisture was lowest in all three sites during May.

Soil pH

The surface soil pH of the three sites was generally higher and fluctuated more than the corresponding subsurface pH (Fig. 3). The subsurface pH of these sites changed very little during the growing season. The decrease in the pH of the soil surface appeared to be correlated to the amount of rainfall. This effect was probably due to the transporting of soluble salts into the subsurface layers by the percolating rain. A decrease in the pH of the surface generally was inversely proportional to the increase in the subsurface pH.

Ion Content of the Soil

Site 1

Osmotic potential measurements of the surface soil were high during July and September. Osmotic potential values were

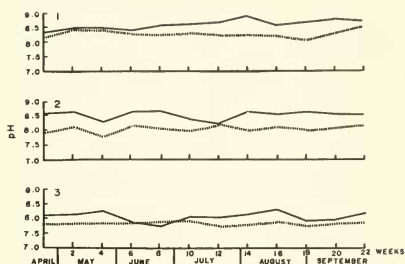


Fig. 3. Soil pH as recorded for three salt desert playas (Sites 1, 2, and 3). The solid lines indicate the plot of the pH for surface samples (upper 2"). The dashed lines indicate the plot of the pH for subsurface samples (6-10").

as high as 135 atm (Fig. 4). Osmotic potential measurements of subsurface soil samples were considerably lower than osmotic potential measurements of the surface. Osmotic potential values for the subsurface soil samples gradually increased. The highest value reached was 48 atm. This value was recorded on 20 September, when the study terminated. Values during the hottest month did not exceed 23 atm.

Individual ion analysis of soil samples from the surface (Fig. 5) and the subsurface layers (Fig. 6) showed that sodium and chloride were the two ions responsible for most of the osmotic potential. The increasing ion accumulation of the soil closely paralleled the increase in osmotic potential previously described. The con-

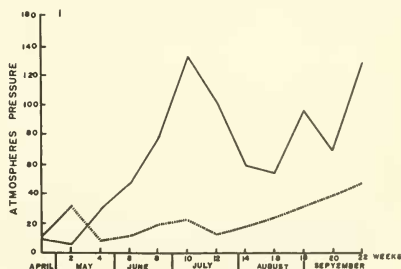


Fig. 4. Osmotic potential of saturated soil paste for a salt desert playa (Site 1) expressed as atmospheres pressure. The solid line indicates the plot of osmotic potential values for the surface soil samples (upper 2"). The dashed line indicates the plot of osmotic potential values for the subsurface samples (6-10").

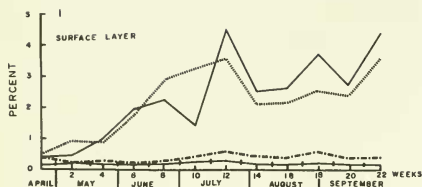


Fig. 5. Ion content of the soil for the surface layer (upper 2") of a desert playa (Site 1) expressed as a percentage of the dry soil. The solid line indicates the percentage of chloride. The dashed line indicates the percentage of sodium. The dash-dotted line indicates the percentage of calcium. The solid vertical-barred line indicates the percentage of potassium.

centrations of sodium and chloride were highest during July and September. The concentration levels of calcium and potassium ions were fairly constant throughout the season. Concentration values seldom exceeded 0.5 percent of the dry soil weight in either the surface or the subsurface layers.

Site 2

Osmotic potential values for the surface layer samples were uniform and high (over 130 atm) throughout the season with the exception of a substantial decrease on 29 August, when values dropped to 80 atm (Fig. 7). The subsurface values steadily increased throughout the growing season to a high of about 96 atm on 20 September. In most cases osmotic potential values of the subsurface soil samples were 50 to 100 atm lower than osmotic potential values of the surface soil samples. Thus, roots near the surface would

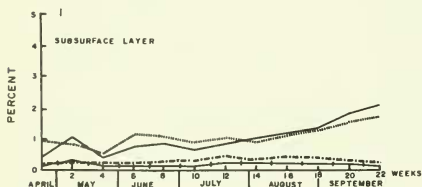


Fig. 6. Ion content of the soil for the subsurface layer (6-10") of a salt desert playa (Site 1) expressed as a percentage of the dry soil. The solid line indicates the percentage of chloride. The dashed line indicates the percentage of sodium. The dash-dotted line indicates the percentage of calcium. The solid vertical-barred line indicates the percentage of potassium.

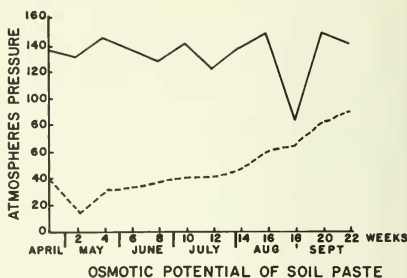


Fig. 7. Osmotic potential of saturated soil paste for a salt desert playa (Site 2) expressed as atmospheres pressure. The solid line indicates the plot of osmotic potential values for the surface soil samples (upper 2"). The dashed line indicates the plot of osmotic potential values for the subsurface soil samples (6-10").

be in an environment of higher moisture stress than deeper roots.

Ion analysis of the surface layer soil samples showed that sodium and chloride ions were responsible for most of the osmotic potential of the soil samples (Fig. 8). The calcium ion concentration of the surface layer for this site was considerably higher than for Site 1. The subsurface calcium and potassium ion concentrations were comparable with other sites and rarely exceeded 0.5 percent of the soil dry weight (Fig. 9). The combined ion concentration in the subsurface layer increased gradually over the growing season and reached a peak of about 6 percent soluble salts on 20 September.

Site 3

Osmotic potential measurements of soil samples on this site gradually increased in both the surface and subsurface layers. Measurements were highest on 20 July and 20 September (Fig. 10) and were comparable with measurements from Site 2, both of which were considerably higher than Site 1.

Chloride ion content from the surface layer fluctuated considerably, but the sodium content was more stable (Fig. 11). The major increase in osmotic potential of the subsurface layer from 20 July through 20 September was due chiefly to the chloride ion content. The calcium ion concentration level of this site was considerably higher than Site 1 and not as high as Site 2. The potassium ion concentration level was less than 0.5 percent

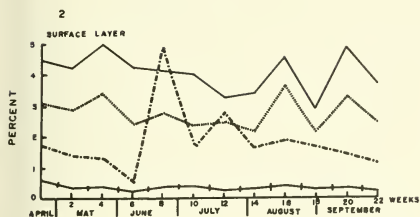


Fig. 8. Ion content of the soil for the surface layer (upper 2") of a salt desert playa (Site 2) expressed as a percentage of the dry soil. The solid line indicates the percentage of chloride. The dashed line indicates the percentage of sodium. The dash-dotted line indicates the percentage of calcium. The solid vertical-barred line indicates the percentage of potassium.

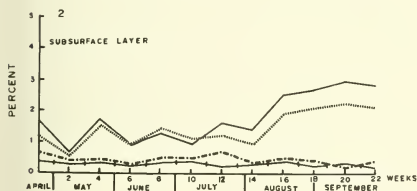


Fig. 9. Ion content of the soil for the subsurface layer (6-10") of a salt desert playa (Site 2) expressed as a percentage of the dry soil. The solid line indicates the percentage of chloride. The dashed line indicates the percentage of sodium. The dash-dotted line indicates the percentage of calcium. The solid vertical-barred line indicates the percentage of potassium.

and did not fluctuate significantly. The concentration level gradually increased to a peak of 0.5 percent on 20 July and then gradually decreased to 0.3 percent on 20 September. Concentrations of sodium and chloride ions in the subsurface soil samples gradually increased (Fig. 12). Calcium and potassium ion concentrations in this layer remained low and relatively constant through the growing season; these ion concentrations were comparable to ion concentrations of the other sites.

Ion Content in Salicornia

Site 1

The chloride ion content in *Salicornia* tissues remained constant throughout most of the growing season but increased slightly in April (Fig. 13). This increase was followed by a stabilization of the con-

centration at about 12 percent of the dry weight. Sodium ion concentration gradually increased from about 4.2 to 9 percent, while potassium ion concentration decreased throughout the season from 2.2 to 1 percent.

Site 2

The chloride content gradually increased from 14.2 to 16.1 percent at the end of the growing season (Fig. 14). Increase in the sodium content was proportional to the increase in the chloride content and was 10.2 percent at the end of the growing season. The potassium ion concentration increased from 4.5 to 7.5 percent and was closely correlated to decreases in the sodium ion concentration.

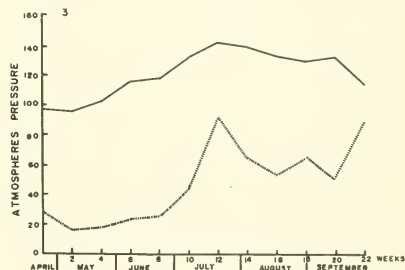


Fig. 10. Osmotic potential of saturated soil paste for a salt desert playa (Site 3) expressed as atmospheres pressure. The solid line indicates the plot of osmotic potential values for the surface soil samples (upper 2"). The dashed line indicates the plot of osmotic potential values for the subsurface samples (6-10").

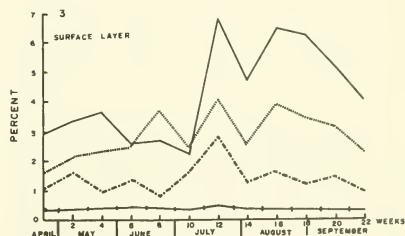


Fig. 11. Ion content of the soil for the surface layer (upper 2") of a salt desert playa (Site 3) expressed as a percentage of the dry soil. The solid line indicates the percentage of chloride. The dashed line indicates the percentage of sodium. The dash-dotted line indicates the percentage of calcium. The solid vertical-barred line indicates the percentage of potassium.

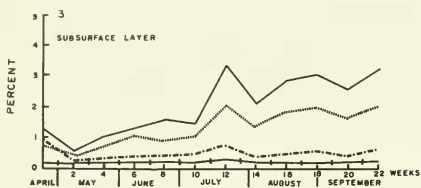


Fig. 12. Ion content of the soil for the subsurface layer of a salt desert playa (Site 3) expressed as a percentage of the dry soil. The solid line indicates the percentage of chloride. The dashed line indicates the percentage of sodium. The dash-dotted line indicates the percentage of calcium. The solid vertical-barred line indicates the percentage potassium.

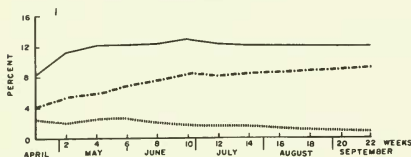


Fig. 13. Ion content in *Salicornia pacifica* (Site 1) expressed as a percentage of the dry weight. The solid line indicates the plot of the percentage values for chloride ions. The dash-dotted line indicates the plot of the percentage values for sodium ions. The dashed line indicates the plot of the percentage values for potassium ions.

Site 3

The ion content in *Salicornia* tissues in this site showed a decrease in chloride, sodium, and potassium throughout the season (Fig. 15). The chloride content ranged from 16 percent on 1 May to 12.4 percent on 20 September. The sodium content ranged from 11 percent on 1 May to 7.6 percent on 20 September. The potassium content ranged from 4.8 percent on 1 May to 2.1 percent on 20 September.

Osmotic Potentials in *Salicornia*

Early in the investigation it was discovered that each internode of the plant was osmotically different from other internodes of the same plant. Freezing-point depression measurements showed that osmotic potential values increased from the base of the aerial shoot upward to the top of the plant (Table 2). The lowest internodes near the base generally had a lower osmotic potential than internodes near the middle of the plant. In some cases there was as much as 15 atm

difference between two regions (inner and outer) of the cortex, although usually the difference was only about 5 atm (Table 2). Because of the complexity of such differences in osmotic potential readings, only periodic measurements were made on the plants. The measurements ranged from a low of about 80 atm in May to about 130 atm to 150 atm in mid-July and August. However, the average was about 90 to 100 atm.

Crude Protein Analysis

Crude protein analysis showed a gradual decrease in the total crude protein content in the plants from all three sites from 1 April through 30 July. Crude protein decreased from 20 to 8 percent on a dry weight basis. From 30 July through 20 September the content remained about 8 percent.

Phenology and Morphology

Growth of *S. pacifica* usually begins with development of the subterranean or

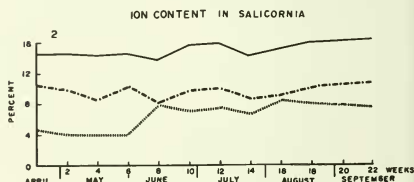


Fig. 14. Ion content in *Salicornia pacifica* (Site 2) expressed as a percentage of the dry weight. The solid line indicates the plot of the percentage values for chloride ions. The dash-dotted line indicates the plot of the percentage values for sodium ions. The dashed line indicates the plot of the percentage values for potassium ions.

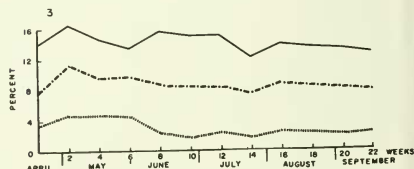


Fig. 15. Ion content in *Salicornia pacifica* (Site 3) expressed as a percentage of the dry weight. The solid line indicates the plot of the percentage values for chloride ions. The dash-dotted line indicates the plot of the percentage values for sodium ions. The dashed line indicates the plot of the percentage values for potassium ions.

TABLE 2. Osmotic potentials of four different *S. pacifica* plants showing the values (atm) of the outer and inner "cortex" tissues from the bottom of the shoot (Node 1) to the top of the shoot (Node 5).

Node	Plant A		Plant B		Plant C		Plant D	
	Inner	Outer	Inner	Outer	Inner	Outer	Inner	Outer
1	76	76	81	81	73	73	84	89
2	69	89	57	75	61	80	64	74
3	71	86	93	86	83	96	71	74
4	67	67	96	106	68	83	73	79
5	106	130	96	106	103	108	84	88
6	89	92	----	----	93	108	----	----
7	106	112	----	----	----	----	----	----

near-subterranean axillary buds of older shoots that start to grow in March and emerge in late April or early May. Flowering occurs in mid-June and is generally completed in July.

By late August lower internodes begin to wither and die sequentially from the base of the shoot to the tip (Fig. 16). Occasionally internodes may become injured or for other reasons may wither and die. The central stele continues to function in a normal manner. Seed-producing internodes are the last to die (Fig. 16). It is not known whether the internodes die strictly by senescence, whether accumulation of additional salts in these areas causes death, or whether death is related to some other phenomenon.

The seeds are shed in October and November. A few seeds adhere to the mother plant until rain or heavy snows separate them. Seeds are protected by a bulky, lightweight seed coat that aids in dispersal and absorption of moisture.

Seasonal Variations of the Environment

Temperatures were highest during July, while relative humidity was lowest during July and August. These high temperatures would cause increased moisture stress.

The toxicity of salts increases with the temperature, according to Kaho (1926) and Waisel (1972). The high moisture content of the soil and the subsequent evaporation may have had a cooling effect upon the temperature of the soil. Both lower temperatures and high relative humidity would have a favorable effect upon plant survival.

At all three sites there was an increase in moisture stress throughout the season primarily due to increases in salt from underground sources and slight decreases in soil moisture. Soil moisture of 25 to 35 percent is perhaps an important fac-

tor in maintaining *S. pacifica* in the environment.

Sodium and chloride were the two principal ions responsible for increases in osmotic potential of soil samples. They were also responsible for 85 to 95 percent of the osmotic potential of *S. pacifica*. Harris (1915) considered NaCl the most toxic of several soluble salts but concluded that salt mixtures were not as toxic in soils as in culture solutions.

The salt concentration of the soil surface layers was considerably higher than the salt concentration in the rooting layers. Soil surface layers were often encrusted with deposits of white salt, which gave the impression that the plants were surrounded by extremely high concentrations of salt when, in fact, the rooting zones or layers were only moderately saline. This observation was also reported by Wiesel (1972). The wicking action caused by evaporation of water resulted in salt crystallization at the surface, which removed salts from the rooting layers and provided a unique environmental niche for *S. pacifica* to occupy. Succulents such as *Salicornia* appear to lose the function of portions of their fleshy cortex and leaves (Fig. 16), yet the vascular system continues to function for the upper fleshy tissue (Fig. 16). The thick cuticle and waxy layer of the plants and the active phellogen of the central stele appear to protect the upper shoots from the more severe environmental stresses.

The soil pH was relatively stable throughout the growing season in all three sites. The surface soil pH of each site was about one-half pH unit higher than the subsurface pH. Decreases in the pH of the surface layers were proportional to increases in pH of the subsurface layer. Conversely, increases in the pH on the surface layer were proportional to de-

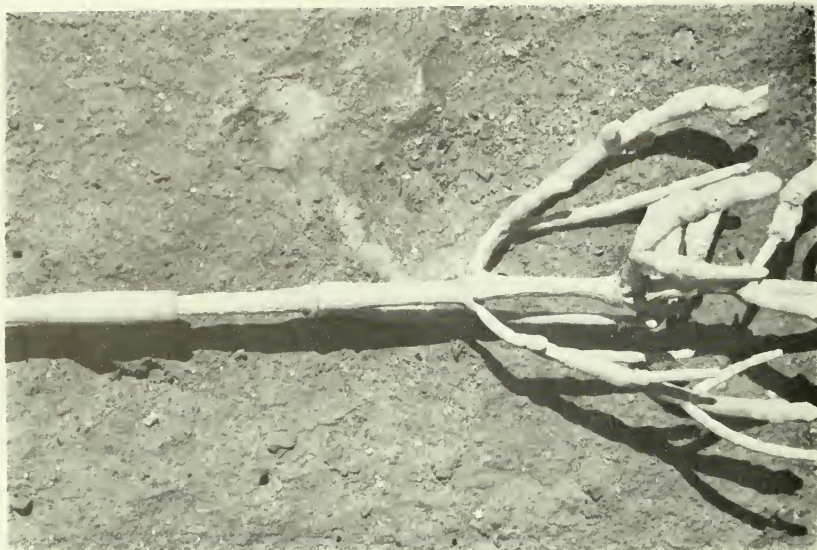


Fig. 16. Shoots of *Salicornia pacifica* showing healthy fleshy portions of stem above dead fleshy sections of cortex.

creases in the pH of the subsurface layer. Calcium ion concentrations in the surface layers were considerably higher at Sites 2 and 3 than at Site 1. Soil pH at Sites 2 and 3 was significantly lower than at Site 1. The pH may have been indirectly affected by the calcium concentration or may have been related to the algal covering of the soil surface in Site 1.

Ecological Interactions and Plant Distribution

There appear to be two groups of thought explaining the restriction of *Salicornia* to a saline environment. New-wohner (1938) stated that halophytes fail to succeed in fresh-water habitats because of competition with other species. This idea was supported by Stalter and Batson (1969), who stated that survival and growth rate data of transplanted salt marsh vegetation suggest that several species of halophytes (*S. virginica* included) can tolerate conditions not found in their usual zones. Montfort *et al.* (1927), on the other hand, claimed that this explanation of plant distribution must be displaced by the concept of "direct ecolog-

ical salt action." He pointed out that *S. herbacea* has an optimum growth between 1.5 and 3 percent salt. Webb (1966) also pointed out that *Salicornia* plants grown without salt soon die. Waisel (1972) stated that the proportion of chlorides to sulfates and the total salt content were important in determining distribution. For example, *S. herbacea* was more sensitive to a high proportion of sulfates than was *Aster tripolium*.

The fact that Site 1 is an ecotone between *S. pacifica* and *Distichlis stricta* suggests that differences in this site compared with the other two sites would provide information regarding some parameters of *S. pacifica*. *Distichlis stricta* in this site appears to tolerate a higher pH than *S. pacifica* and may survive in pH values from 8.0 to 9.0. The soil pH apparently affects the availability of nutrients. At pH values over 7 the availability of manganese, iron, copper, molybdenum, and zinc declines (Buckman and Brady, 1969). At high pH values phosphorus forms insoluble complexes of calcium that are unavailable to the plants (Buckman and Brady, 1969). Levitt (1972) also pointed out that *Allenrolfea*

occidentalis and *S. subterminalis* are highly resistant to salt but sensitive to alkalinity. A change from saline to sodic soils may kill these plants. Site 3, where *S. pacifica* cover and production were the highest, had an average pH of 7.7 and a moisture content of 32 percent. At Site 1 reduction in the soil moisture and the increase in the total concentration of salts of the subsurface soil layers during the season apparently also favored growth of *D. stricta* over *S. pacifica*. *Distichlis stricta* appears to be a better competitor for low soil moisture than *S. pacifica*. It seems probable that during the initial adaptation of *Salicornia* to the saline environment competition played a major role in determining plant distribution. As natural selection of *Salicornia* occurred, adaptations allowing the plant to maintain itself in an optimal salt concentration were reinforced. Plasticity could be reduced and that portion of the gene pool lost that allowed the plant to move back into non-saline areas. As such selective forces would be localized, it would be improper to generalize and say that all species of *Salicornia* have optimum growth at high salt concentration. The variations in salt concentrations that yield optimum growth of *Salicornia* would bear this out (Halket, 1915; Webb, 1966; Levitt, 1972; Waisel, 1972).

The Nature of the Fleshy Stem

Anatomical investigations with light microscopy indicate that as internodes mature or become injured a phellogen that produces fibers and suberized cells is formed in the central stelar region (unpublished results). These cells seal off the conductive tissues from water and nutritive loss as the internodes wither and die. This development would protect the plant when the salt and moisture stresses are the greatest near the surface in July and August.

Osmotic potential measurements of the plants indicated that each internode is probably osmotically independent from other internodes. This would allow the plant to survive in the environment if a few of the internodes were attacked and destroyed by insects or disease. Hill (1908) showed that osmotic adaptation differs not only between species but also between organs and even between cells.

In his investigation root hairs varied greatly in this respect, even in the same individual plant. Measurements of freezing-point depression of *S. pacifica* internodes indicated that at least two areas of osmotically different tissues were present within one internode, corresponding to the inner "cortex" and outer chlorenchyma tissues. Osmometer measurements on dissected portions of these tissues indicated that the chlorenchyma tissue had a higher osmotic potential. Scholander *et al.* (1966) suggested that xylem sap of *S. pacifica* may contain very little salt as freezing-point depression of *S. pacifica* sap was found to approach freezing-point depression of pure water. Since chloride ions were equally distributed in these two tissues (unpublished data), the difference was probably due to sodium ions or sugars and other organic molecules that were produced by chloroplasts in the immediate vicinity. Steiner (1935) has shown that chloride ions account for 67 to 88 percent of the increase in osmotic potential of different species of salt marsh plants, whereas other osmotically active substances had only negligible effects. This increase in chloride was shown to account for increases in the osmotic potential of the entire plant. This does not rule out the possibility that differences in osmotic potentials of individual tissues might be due to other osmotically active substances. Increase in the chloride and sodium content of the succulent tissues appears to be the primary means of osmotic adaptation whereby the plant can survive under increased salt and moisture stress. Sodium and chloride ions account for 85 to 95 percent of the osmotic potential of *S. pacifica*. These results agree with the findings of Harward and McNulty (1965) and Scholander *et al.* (1966). Ion analysis of *S. pacifica* tissues in Site 1 indicated that increases in osmotic potential were due to increases in Na^+ but not Cl^- . Increases in osmotic potential at Site 2 were due to both Na^+ and Cl^- . However, at Site 3 there was a decrease in both Na^+ and Cl^- . As the concentration of the soil salts increased, causing an increase in moisture stress, osmotic potential of the plant also increased. This increase was due chiefly to ions other than Na^+ and Cl^- or sugars and other organic molecules.

Ion analysis of *S. pacifica* tissues showed that the chloride ion was present

in higher concentrations than sodium or potassium ions. Azizbekova and Babaeva (1970) found that the amount of absorbed Na^+ , Cl^- , and Mg^{++} in *Salicornia* increased with increasing salt concentrations.

During the period of greatest moisture stress, from July through September, the percentage of crude protein in *S. pacifica* for all three sites remained constant at about 8 percent of the dry weight. The percentage ion content of sodium, potassium, and chloride also remained relatively constant throughout the growing season, even when environmental stresses fluctuated considerably.

The metabolism of *S. pacifica* functioned even with changes in the ionic balance and concentration of ions in the plant. The changes, however, were gradual.

REFERENCES

- ADAMS, D. A. 1963. Factors influencing vascular plant zonation in North Carolina salt marshes. *Ecology* 44:445-456.
- ADRIANI, M. J. 1958. Halophyten. *Encycl. Plant Physiol.* 4:709-736.
- ARNOLD, A. 1955. Die Bedeutung der Chlorionen für die Pflanze. Guxtav Fischer. Jean.
- BERNSTEIN, L. 1961. Osmotic adjustment of plants to saline media. I Steady state. *Amer. J. Bot.* 48:909-918.
- BOWEN, G. D., AND A. D. ROVIRA. 1966. Microbial factor in short-term phosphate uptake studies with plant roots. *Nature* 211:665-666.
- BUCKMAN O., AND C. BRADY. 1969. The nature and properties of soils. Macmillan Company, London.
- CARY, J. W., AND H. D. FISCHER. 1969. Plant moisture stress: a portable freezing-point meter compared with the psychrometer. *Agron. J.* 61:302-304.
- . 1971. Plant water potential gradients measured in the field by freezing point. *Physiol. Plant.* 24:396-401.
- CHAPMAN, V. J. 1960. Salt marshes and salt deserts of the world. Lenard Hill Books Ltd., London.
- FISHER, H. D. 1972. An inexpensive method of determining plant moisture stress using freezing-point depression. *Soil Sci.* 113: 383-385.
- GAUCH, H. G., AND F. M. EATON. 1942. Effect of saline substrate on hourly levels of carbohydrates and inorganic constituents of barley plant. *Plant Physiol.* 17:422-434.
- HALKET, A. C. 1915. The effect of salt on the growth of *Salicornia* Ann. Bot. 29:143-154.
- HANSEN, D. J., AND D. J. WEBER. 1974. Application of freezing point depression for the determination of osmotic potential of solutions and soils in saline areas. *Soil Sci.* 117:191-193.
- HARRIS, F. S. 1915. Effect of alkali salts in soils on the germination and growth of crops. *J. Agr. Res.* 15:287-319.
- HARWARD, M. R., AND I. McNULTY. 1965. Seasonal changes in ionic balance in *Salicornia rubra*. *Proc. Utah Acad. Sci., Arts, Letters* 42:65-69.
- HILL, T. G. 1908. Observations on the osmotic properties of the root hairs of certain salt marsh plants. *New Phytol.* 7:133-142.
- HORWITZ, W. 1970. Official methods of analysis of the association of official analytical chemists. Association of Official Analytical Chemists, Washington, D.C.
- KAHO, H. 1926. Über den Einfluss der Temperatur auf die koagulierende Wirkung einiger Alkalisalze auf das Pflanzenplasma. *VIII Biochem. Z.* 167:182-194.
- LEVITT, J. 1972. Responses of plants to environmental stress. Academic Press, New York.
- MANUS/FISKE. 1972. Chlor-o-counter instructions for use. Fiske Associates, Inc., Massachusetts.
- MONTFORT C., AND W. BRANDRUP. 1927. Physiologische und Pflanzengeographische Seesalzwirkungen. I. Ökologische Studien über Keimung und erste Entwicklung bei Halophyten. *Jahrb. Wiss. Bot.* 66:902-946.
- NEUWOHNER, W. 1938. Der tagliche Verlant von Assimilation und Atmung beim emign Halophyten. *Planta* 28:644-679. As abstracted by Biological Abstracts. 1939. Entry No. 1842.
- PERKIN-ELMER. 1970. Analytical methods for atomic absorption spectrophotometry. Norwalk, Connecticut.
- SCHOLANDER, P. F., E. D. BRADSTREET, H. T. HAMMEL, AND E. A. HEMMINGSEN. 1966. Sap concentrations in halophytes and some other plants. *Plant Physiol.* 41:529-532.
- STALTER, R., AND W. T. BATSON. 1969. Transplantation of salt marsh vegetation, Georgetown. *South Carolina. Ecology* 50:1087-1089.
- STEINER, M. 1935. Zur Ökologie der Salz-marschen der nordöstlichen Vereinigten Staaten von Nordamerika. *Jahrb. Wiss. Bot.* 81:94-202.
- UNGAR, I. A., W. HOGAN, AND M. MCCLELLAND. 1961. Plant communities of saline soils at Lincoln, Nebraska. *Amer. Midl. Natur.* 82:564-577.
- WASEL, Y. 1972. Biology of halophytes. Academic Press, New York.
- WEBB, K. L. 1966. NaCl effect on growth and transpiration in *Salicornia bigelovii*, a salt marsh halophyte. *Plant Soil* 24:261-265.
- YABE, A., G. KUSE, T. MURATA, AND H. TAKADA. 1965. Physiology of halophytes I. The osmotic value of leaves and the osmotic role of each ion in cell sap. *Physiol. Ecol.* 13:25-33.